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Barnacle geese *Branta leucopsis* breed on small islands in the Kongsfjorden area, Spitsbergen. Shortly after hatching, families approach feeding sites at the mainland coast in the close surroundings of the village Ny-Ålesund. The goslings are subject to predation by arctic foxes *Alopex lagopus* throughout the whole brood-rearing period. This study compares the choice of foraging areas in a year with fox predation with years with no foxes present. Observations of ringed individuals show that the use of tundra sites by families decreases in a year with foxes present. In such a year, foraging of goose families is limited to sites in the proximity of open water. Non-breeders are not affected in their choice of foraging areas by the presence of arctic foxes and prefer sites along lake shores during wing moult. Habitats vary in food quality and quantity according to the dominant vegetation type. Approximately 85% of the diet of geese grazing on meadows within the village and on tundra sites consists of graminoids and dicots, whereas geese grazing on lake shores consume up to 35% moss. A grass-dominated diet yields good digestibility and a favourable protein gain, compared to moss which is of lower quality. In a fox year, predation risk restricts goose families to a small range of safe foraging sites where grazing pressure is high. Data on slower gosling growth support the hypothesis of food limitation and competition among families in such a year.

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Introduction

In high arctic breeding grounds, many goose species are confronted with substantial constraints concerning favourable food sources. Because of the shortness of growing seasons at high latitudes, the productivity of arctic grassland ecosystems is low (Gauthier et al. 1997). Plant cover is often patchy and potential food plants vary considerably in quality; digestibility and protein content of food plants increase from moss to dicots to monocots (Prop & Vulink 1992; Prop & de Vries 1993). Grass species rank highest in crude protein content (15–25%) and in digestibility (up to 60%); mosses only yield 10% crude protein and are highly indigestible due to a fibre content of 80% (Staaland et al. 1983; Prop & Vulink 1992; Gaddalah & Jefferies 1995). Although a graminoid-based diet is desirable for non-breeders and family birds alike, Prop & Vulink (1992) showed that adult geese coped with high moss contents in their diet by prolonged food retention. During the continuous light regime of the arctic sites, adult barnacle geese *Branta leucopsis* increased the retention time of ingested food and thereby raised digestibility.

The circumstances are different for geese which raise goslings. Gosling growth of different goose species has been shown to be susceptible to slight changes in food quality (Lindholm et al. 1994; Gadallah & Jefferies 1995) and availability of favourable food plants (Cooch et al. 1993). In addition, growth conditions during the gosling period affect adult size and survival (Owen & Black 1989; Sedinger et al. 1995; Loonen et al. 1997; Loonen et al. in press). The small digestive tracts of goslings are neither able to cope with long retention times during food processing (Sedinger & Raveling 1988) nor can they compensate for low nitrogen contents of food plants by increasing their intake (Manseau & Gauthier 1993). Therefore, family birds must mainly feed on nitrogen-rich forage with low fibre content as is provided by a grass-dominated diet.

The short, high arctic summer and approaching autumn migration require profitable foraging decisions to be made by all arctic breeding geese during the moulting and brood-rearing periods.

Predation risk is one important parameter that affects these foraging decisions. Predators influence the fitness of individuals either directly by attacking the offspring or the individuals themselves, or indirectly by affecting the relative accessibility of foraging sites (Lima & Dill 1990). Arctic foxes and glaucous gulls *Larus hyperboreus* are considered important predators in northern ecosystems (Mehlum 1991; Stickney 1991; Birkhead & Nettleship 1995). Syroechkovskiy et al. (1991) discuss the breeding success of different arctic goose species and lemming-cycle-related predation pressure by foxes in northern Russia. In a colony of Alaskan breeding black brant *Branta bernicla nigricans*, nesting success was increased by removal of foxes from the area (Anthony et al. 1991). Most of the above-mentioned studies, however, focus on the direct influences of predators on breeding performance and hatchling mortality. Little is known about the influence of predation on the choice of foraging areas in terrestrial ecosystems (see Lima & Dill 1990). Our study concentrates on the indirect effects of the presence of a predator in an area. We compare the habitat use of barnacle geese in years with and without predation by arctic foxes. This comparison is possible in the Kongsfjorden colony due to the philopatry of family birds as well as non-breeders to a limited area of 10 km^2 during brood-rearing and wing moult.

Study area

This study was carried out in the surroundings of the village Ny-Ålesund in Kongsfjorden (78°55′N, 11°56′E) on the island of Spitsbergen in the Svalbard archipelago (Fig. 1). The study area (10 km^2) is bounded by the fjord to the north, by mountains to the south and by glacial gravel fields to the east and west. It comprises different vegetation types which can be grouped into three habitat types:

(1) *meadows*, which are characterised by a well-drained sandy soil and dominated by grasses such as *Poa arctica* and *Deschampsia alpina* (total area 0.05 km^2). This habitat type can only be found in the centre of the village.

(2) *lake shores*, which are characterised by a wet undrained soil and dominated by moss vegetation with sparse stands of *Poa arctica* (total area 1.34 km^2).

(3) *tundra*, which is characterised by lichens and dicots such as *Salix polaris* and *Saxifraga oppositifolia* and scattered stands of various monocotyledons (total area 6.14 km^2). This dominant habitat type is located in a band of an average width of 1 km between mountains and fjord.

The barnacle goose breeding colony in Kongsfjorden was established in the early 1980s (Prestrud et al. 1989). In 1996, a count resulted in approximately 700 adult geese (Loonen et al., this volume). To evade predation by arctic foxes, most of the geese nest on small islands in the fjord. Goslings hatch during the first two weeks of July, with peak hatching around 7 July (Tombre 1995). Families approach feeding sites along the mainland coast within the first week after hatching. Groups of families and of moulting non-breeders concentrate in the close vicinity of the village and surrounding tundra throughout the whole moulting and brood-rearing period in July and August.

Methods

Observations on ringed individuals

Since 1987, barnacle geese of the Kongsfjorden colony have been caught during wing moult and marked individually with coded colour leg rings (Loonen et al., this volume). The majority of the breeding pairs is recognisable by leg rings of at least one partner. The data analysed in this paper were collected during the months of July and August of the years 1991, 1993 and 1996. On a daily basis, ring readings of all geese present in the focal study area (2 km^2 in the vicinity of Ny-Ålesund) were carried out. The rest of the study area was covered during weekly censuses. Recorded parameters for ringed birds were family status and used habitat type.

Predation pressure

Post-hatching predation of goslings by arctic foxes on the mainland shore varied considerably

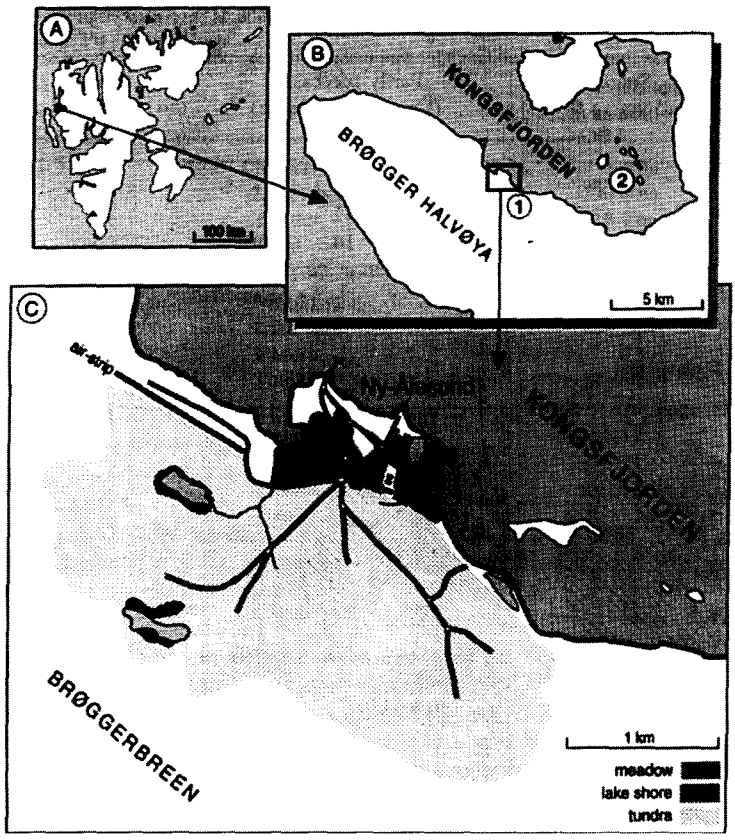

Fig. 1. The study site. A. Svalbard. B. Kongsfjorden with the village Ny-Ålesund (1) and the breeding islands (2). C. Focal study site with three distinguished habitat types.

between years. In 1991 and 1996, no foxes were recorded in Kongsfjorden. We refer to these years as fox-free. In 1993, at least three foxes were observed on the southern side of Kongsfjorden and one den was found. However, no foxes approached the main breeding island and the hatching success of the geese was hardly affected by fox predation. To calculate the influence of fox predation on the fledging success of goslings, we compared family sizes of ringed individuals at their first sighting on the mainland shore in July with family sizes of the last sighting in August. This method corrects for early hatchling predation by glaucous gulls on the breeding islands.

Vegetation sampling and dropping analysis

We measured the standing crop of graminoids by using a semi-random sampling technique whereby five samples were collected per sampling effort in all three habitat types. Within a movable metal frame (covering an area of 20 by 20 cm), all grass shoots were clipped, sorted into living and dead material, dried for 48 h at 60°C in a drying stove and weighed. Differences in species composition of graminoid standing crop among the three habitats were not taken into account and we refer to all species collectively as monocots in this study.

For dietary analysis five faeces samples each containing five droppings of adult geese were collected in all three habitat types concurrently with measurements of graminoid biomass. The samples were dried for 48 h at 60°C, blended and washed over a 0.1 mm sieve. At random, 100 cell fragments were microscopically determined to genus level and measured in size. The composition of the diet was determined according to the occurrence and the size of plant fragments. These surface measurements of plant fragments in the

Table 1. Brood rearing success of ringed female barnacle geese in the period from hatching to fledging. (1991 and 1996 without fox predation (−), 1993 with fox predation (+))

Year	Total number of females	Successful (all young fledge) %	Partly successful (some young fledge) %	Failed (no young fledge) %
1991 −	60	62	35	3
1993 +	90	13	42	45
1996 −	100	79	16	5

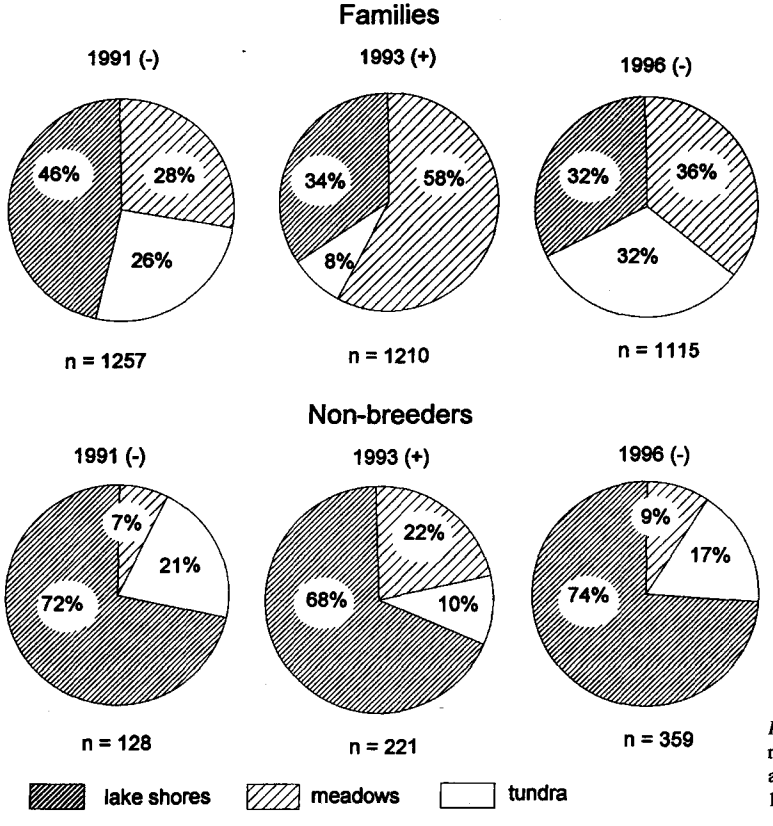

Fig. 2. Habitat use of families and non-breeders in three years: 1991 and 1996, fox-free years (−), and 1993, fox predation year (+).

diet counterbalance differential fragmentation of plant species in the goose gut (for technique see e.g. Owen 1975). During further analysis, food species were grouped as monocots, dicots and mosses. Data on standing crop and goose diet were collected in the first week of August 1997, when non-breeders and families were both present on the mainland sites in the breeding season.

Habitat availability and safety

By means of an OTT planimeter, the surface areas of the three habitat types used were measured on vegetation maps (Brattbakk 1981a, b) and on false colour satellite pictures. The distances of the different habitat types from the respectively

Table 2. Extrapolation of available grass biomass for brood-rearing areas for barnacle geese in Ny-Ålesund, Spitsbergen. Data are based on Figs. 2 and 3B.

Year	Area type	Area size and availability	Grass biomass (dry weight)
1991	Meadows	5.4 ha	27.16 kg
	Lake shores	134.2 ha	150.84 kg
	Tundra	613.7 ha	1669.26 kg
	Total	753.3 ha	1847.26 kg
1993	Meadows	5.4 ha	27.16 kg
	Lake shores	134.2 ha	150.84 kg
	Tundra	0 ha	0 kg
	Total	139.6 ha	178.00 kg
1996	Meadows	5.4 ha	27.16 kg
	Lake shores	134.2 ha	150.84 kg
	Tundra	613.7 ha	1669.26 kg
	Total	753.3 ha	1847.26 kg

closest water body in all areas were measured on the same maps. Maximum and minimum distances contributed to the values shown in Fig. 3A.

Data analysis

To analyse the data on area use, we included observations of female birds from the period of 15 July (8 days after the hatch peak on the breeding islands) to 15 August (before non-breeders left the area). We accounted for an interval of at least 12 hours between repeated sightings of the same ringed bird to enable individuals to move among habitat types, and we assumed independence between these observations. Repeated sightings of the same individual within a shorter time period were not included in the analysis. Birds were classified as family birds if they had a partner and were accompanied by at least one gosling. The category 'non-breeders' was applied to geese with or without a partner and which were neither accompanied by goslings nor registered as 'breeding birds' from censuses on the breeding islands (Tombre, unpubl. data). Failed breeders, which lost all young within the period from hatching to fledging, were not included in the analysis.

Statistical analysis

Chi-square statistics were applied to the data on the habitat use of ringed birds. Data on standing crop were log-transformed and tested using a one-way ANOVA and Tukey test. For analysis of differences in diet composition between areas, a one-way ANOVA and Tukey test were applied to the weighed data. For statistical analysis the program SPSS/PC+ was used.

Results

Influence of fox predation on fledging success

Table 1 compares the breeding success of female geese in two fox-free years (1991 and 1996) with that of a typical fox year (1993). In the fox year, 45% of the females had lost their goslings by the end of the brood-rearing period. Another 42% of the families were reduced in size. Only 13% of all females raised the entire brood size successfully. In fox-free years, respectively 62% or 79% of all females raised the entire number of goslings successfully.

Habitat choice of families and non-breeders

Table 2 presents data on the size of the available areas in different years (assuming that tundra sites are inaccessible in fox years). The available foraging area is five times larger in fox-free years. Area use of families varied significantly between a fox year and fox-free years (Fig. 2A, 1993 vs. 1991: $\chi^2 = 252.0$, df = 2, $p < 0.001$; 1993 vs. 1996: $\chi^2 = 222.9$, df = 2, $p < 0.001$). In 1996, a year without foxes, families used meadows, tundra sites and lake shores equally as foraging sites. In 1993, a fox year, the use of tundra sites was restricted to 8% of all family sightings. The use of lake shores remained approximately the same, but the utilisation of meadows increased by almost 20% in a fox year. Moulting non-breeders used mainly lake shore vegetation for foraging, and only 30% of all sightings accounted for the two other habitat types (Fig. 2B). Non-breeders also tended to switch from meadow sites to tundra areas in fox-free years, though these habitats were never preferred as much as by family birds (1993 vs. 1991: $\chi^2 = 17.9$, df = 2, $p < 0.01$; 1993 vs. 1996: $\chi^2 = 24.5$, df = 2, $p < 0.01$).

Safety, food availability and dietary considerations

The predation risk of the three habitat types was indicated by the distance of foraging sites from the nearest water body (Fig. 3A). Flightless geese had to cover a distance five times greater when escaping from a fox on tundra sites compared to geese feeding on the meadows. The average biomass was low (less than 1 g/m^2) in all three habitat types, and the harvestable standing crop of monocots was not significantly different between meadows, tundra sites and lake shores (Fig. 3B, one-way ANOVA, $p > 0.05$).

For geese foraging on meadow or tundra sites, approximately 80% of the diet consisted of monocots (Fig. 3C). Along lake shores, grasses formed only 50% of the food and mosses accounted for 30% of the diet. The fraction of monocots in the goose diet on meadows and on the tundra differed significantly from that on lake shore vegetation (one-way ANOVA, Tukey test, $F_{2,15} = 14.89$, $p < 0.001$). Dicots played a minor role as a food source in all three habitat types.

Discussion

Fledging success in fox years versus fox-free years

A between-year comparison of the number of females that lost all their young between hatching and fledging reveals that arctic foxes were likely the main cause for this failure. In fox-free years, only a small percentage of families, which managed to escape gull predation on the breeding islands and reached the foraging sites on the mainland, failed completely (Table 1). Families were very vulnerable to fox predation throughout the whole brood-rearing period (own obs.) and were alert for access to possible refuge areas (mainly the water bodies of shallow lakes) whenever arctic foxes approached.

Area choice and dietary considerations of non-breeders

Moulting non-breeders preferred mossy lake shores as main foraging habitat irrespective of the presence of foxes throughout the years (Fig. 2). These areas offered the lowest biomass of monocots compared to the other two habitat types, and dropping analysis revealed a high fraction of mosses in this diet. It is possible, however, that this group of adult geese can compensate for the low digestibility of mosses with a prolonged retention time (Prop & Vulink 1992), allowing them at the same time to profit from the close proximity of the lakes as refuges during their flightless period (Fig. 3A). In addition, non-breeding birds enter the flightless period with better body condition than breeders (unpubl. data) and thus have an energetic margin in balancing their budget. This preference of safety over more favourable conditions represents a trade-off which deserves more detailed study.

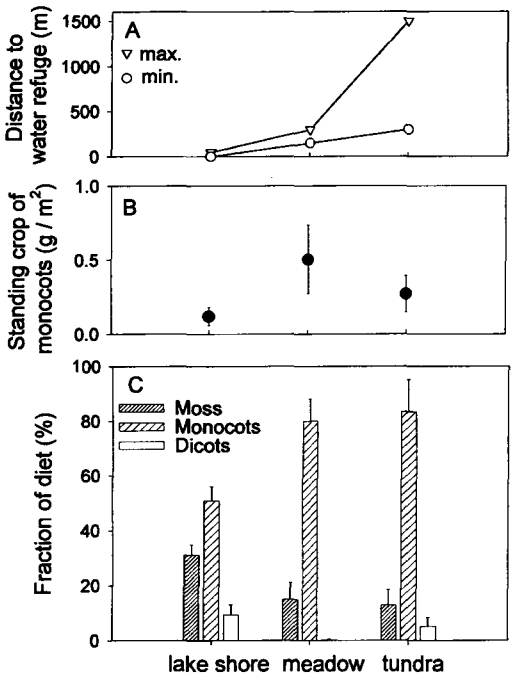

Fig. 3. Site characteristics and goose diet for the three habitat types. A. Maximum and minimum distance to nearest water body. B. Standing crop of living grass biomass (mean, SE, n = 5). C. Fraction of the three main food classes in the diet (mean, SE, n = 5).

Area choice and dietary considerations of families

In all years, mossy lake shore sites account for less than 50% of all sightings of families. Accordingly, families use either tundra or meadow sites in more than 50% of all cases. Both these sites contain vegetation types that grant a graminoid-based diet. The shift of family birds toward tundra sites in fox-free years suggests a strong restriction in years with fox presence to limited, but safe, areas in the proximity of village houses and along lake shores. The available grass biomass on tundra sites is as sparse as on mossy lake shores. The geese, however, seem to be able to compensate for the low standing crop on the tundra and achieve a favourable graminoid-based diet there (Fig. 3C). They most likely forage highly selectively on monocot shoots and make use of the much larger tundra area (Table 2). If we calculate the mean monocot biomass measured in the three habitat types (Fig. 3B) for the whole area size accessible under the two predation scenarios, the calculation results in a 10 times larger amount of available food in years without foxes.

Consequences

Several studies have shown that growing goslings are especially vulnerable to shortages in food availability and quality (e.g. Aubin et al. 1986; Gadallah & Jefferies 1995). Based on results from a supplementary feeding trial with semi-captive goslings of greater snow geese *Anser caerulescens atlantica*, Lindholm et al. (1994) argue that a five to seven day difference in hatching date results in major consequences for growth and survival of the young. In greater snow geese, late broods are faced with a rapid decline in availability and quality of the major food plants during the arctic summer. In addition, late families are probably excluded from favourable foraging sites through mechanisms of intraspecific competition (Dalhaug et al. 1996 for barnacle geese). Hughes et al. (1994) suggest from their study on greater snow geese that experienced, early laying females stay at one foraging site during brood-rearing and force late hatching families to wander to other areas. Our own data suggest a link between predation, restricted area accessibility and intraspecific competition. The aspect of competition is also emphasised by another study on the Kongsfjorden goose population (Loonen et al., this volume). The authors show there that goslings of similar age are approximately 250 grams heavier in years without fox predation than in fox years. The early exhaustion of favourable but limited meadow sites and the absence of alternative foraging areas in a fox year are explanations for the observed weight differences. In a study on lesser snow geese *Anser caerulescens caerulescens*, dispersal behaviour in reaction to deteriorating environmental conditions is advantageous (Cooch et al. 1993). Breeding pairs respond to overcrowding and vegetation degradation in a traditional breeding colony by colonising a new breeding site where they are able to raise heavier and larger goslings. Our study indicates that the presence of a predator in a brood-rearing habitat can reinforce competition and evoke density dependent processes similar to overcrowding in large breeding colonies.

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